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THE NUTRITIVE VALUE OF THE FOOD RESERVE IN COTYLEDONS

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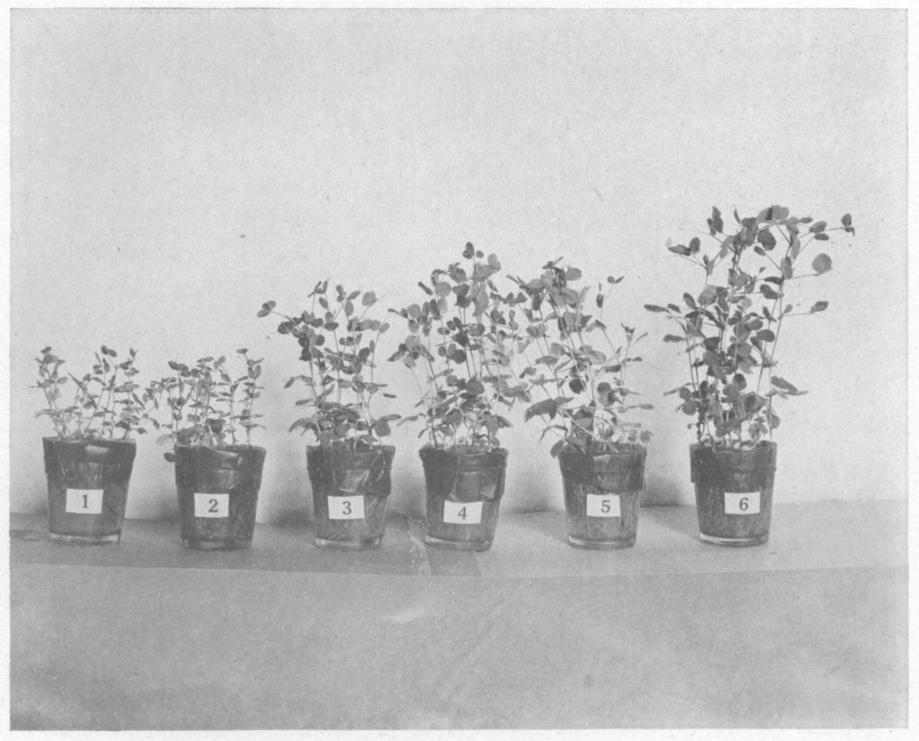
Considerable work has been done in respect to determining the capacity for growth of immature and mature seed-plant embryos separated from the endosperm or from the cotyledons. Yet this work seems to have been of comparatively little significance in ascertaining whether, under any conditions of germination and growth, these natural food reserves may be partially or completely substituted for in establishing the seedling with normal vigor in the soil or in the usual culture solutions. Reference will be made later to some of the more important literature bearing on the questions to be presented in this paper. The data here reported are, however, preliminary and intended primarily to give the results of some experiments (1) demonstrating, in those cases where the cotyledons serve as a food reserve, the striking importance of these seed-leaves in comparison with certain organic substances as a source of food for the normal and vigorous establishment of the young plant under cultural conditions, and (2) suggesting the possibility that carbohydrate or hydrocarbon food material stored outside the embryo, as in the case of corn, may be of far less significance.

Doubtless the assumption has been quite generally made that in the case of peas, beans, and other plants in which the cotyledons furnish practically the entire food reserve these seed-leaves may constitute the chief source of organic food until the first green leaves are developed. It has seemed to the writer that interesting physiological problems might be approached through a critical study of the early food reserves, and preliminary tests with Canada field peas confirmed this assumption. Accordingly, the first series of experiments with Canada field peas and with field corn were made merely to determine quantitatively the extent to which the excision of the cotyledons, or of the food supply stored outside of the embryo and the scutellum, influenced normal growth.

In the case of the Canada field peas the seed were germinated on paraffined wire mesh over tap water, and growth was permitted to proceed in diffuse light until the plumules were well established with unfolding green leaves. Solution cultures were then made in the usual way as especially described in an earlier paper (Duggar, '19). All cultures were therefore arranged in duplicate in tumblers holding about 250 cc., and the seedlings were inserted through holes in paraffined paper covers (peas), or through notches in the corks (corn). Seedlings of uniform size were selected and all cultures were placed in the greenhouse, freely and equally exposed to sunlight. A mineral nutrient solution, designated in the paper referred to above as solution B, was employed. It should be observed that this solution contains not merely all essential ions, including NO_3, but contains these in favorable proportions and concentrations for the promotion of excellent growth. The date of the beginning of the experiment was taken as that on which the cultures were exposed in the greenhouse. At intervals of a day or more apart, the cotyledons of successive pairs of cultures were cut away so as to determine their influence on growth, and the time of excision of the last pair represented the practical exhaustion of these food reserves. In the case of corn the young plantlet with attached scutellum was carefully dissected out from the endosperm, an operation which may be effected with very little difficulty after germination begins. In all other respects the corn cultures were treated in precisely the same manner as the peas. The total green weights of all cultures are given in table I, and the appearance of the peas at the end of the period of observation, 24 days, is shown by pl. 7.

From the results with peas it is clear that for a growth interval of 24 days the removal of the cotyledons after the second day induces a marked depression in the growth rate, and this depression is increasingly less, until, when the removal of the cotyledons occurs after 7 days, the amount of growth is very nearly the same as in the control, with cotyledons intact. Duplication of this experiment with some modifications in the interval led to the conviction that under the conditions the cotyledons are practically exhausted in somewhat less than 10 days. It might be pointed out that the removal of the coty-



DUGGAR—FOOD RESERVE IN COTYLEDONS
(Canada field peas, see table 1)

TABLE I

THE EFFECTS OF THE RESERVE FOOD SUPPLY ON THE GROWTH OF SEEDLINGS

Cult. no.	Field corn, 10 plants, average of duplicate cultures		Canada field peas, 10 plants, average of duplicate cultures		
	Time of excision of endosperm	Total green wt., grams	Cult. no.	Time of excision of cotyledons	Total green wt., grams
1	After 2 days	32.72	1	After 2 days	5.75
2	After 5 days	30.18	2	After 3 days	10.12
3	After 7 days	34.02	3	After 4 days	17.70
4	After 8 days	30.11	4	After 5 days	19.82
5	After 9 days	36.11	5	After 7 days	24.30
6	After 10 days	36.98	6	Control, uncut	25.51

ledons was done in all cases with the greatest care, so that no injury to the seedling would result. The excision was made at a point beyond the stalk of the cotyledons. In the case of corn the results are a little irregular. Nevertheless, there is the suggestion that the removal of the main carbohydrate food supply is not so important a factor in depressing the growth of the young plant. From subsequent incidental experiments I am convinced that there is some effect, but it is neither so marked as in the case of the peas nor does it seem to be so permanent, that is, the effect is not so striking during the further development of the plant.

During the summer of 1919[1] an attempt was made to substitute for the loss of the cotyledons in the case of the peas by the addition of certain organic nitrogen-containing nutrients, and especially by the addition of glycocoll, alanin, sodium asparaginate, and sodium nucleinate. These experiments were carried out under the most favorable conditions for the growth

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[1] This series of experiments and other supplementary studies not yet concluded were carried out at the Coastal Laboratory of the Carnegie Institution of Washington, Carmel, California, and the writer takes this occasion to acknowledge his indebtedness to the Director of Botanical Research, Doctor D. T. MacDougal, for placing at his disposal the facilities of the laboratory and for his cordial coöperation.

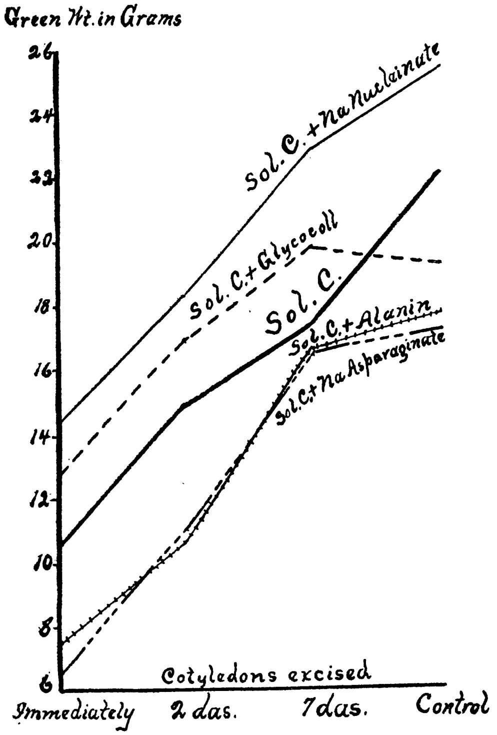

Fig. 1. Green weight quantities of Canada field peas in various solutions as affected by cotyledon excision.

of peas, at a mean temperature of about 15.6° C. The technique was the same as above described, but the use of organic substances in the solutions made it desirable to renew the solutions every 3 or 4 days in order to reduce or control bacterial action. The complete results are shown in table II, and in fig. 1. It will ultimately be necessary to extend the use of organic substances and to repeat this work under pure culture conditions. In fact, a small series of experiments in this direction has already been performed, but inasmuch as these are to constitute a part of a more extended study I will confine myself here to a brief discussion of the data presented below.

In general it will be seen that whatever the medium employed as a nutrient solution the removal of the cotyledons is shown by marked depression in the growth rate. The mineral nutrient solution employed in this case is that which I have in a previous

TABLE II

THE EFFECTS OF THE EXCISION OF THE COTYLEDONS UPON THE GROWTH OF CANADA FIELD PEAS

Cult. no.	Culture medium	Time of excision	Total gr. wt.	Gr. wt. of tops	Gr. wt. of roots	Per cent rel. to cor. cult., sol. C*	Per cent rel. to cult. 4
			10 plants, weight in grams				
1	Solution C	Immediately	10.26	4.97	5.29	100	46
2		After 2 days	14.90	8.75	6.15	100	67
3		After 7 days	17.50	11.64	5.86	100	79
4		Control, uncut	22.11	14.40	7.71	100	100
5	Solution C	Immediately	12.28	7.38	4.90	120	56
6	+	After 2 days	16.90	10.40	6.50	113	76
7	glycocoll	After 7 days	19.81	13.93	5.88	113	90
8	(M/100)	Control, uncut	19.29	13.45	5.84	87	87
9	Solution C	Immediately	6.57	3.92	2.65	64	30
10	+ sodium	After 2 days	11.04	6.68	4.36	74	50
11	asparaginate	After 7 days	16.44	10.09	6.35	94	74
12	(M/100)	Control, uncut	17.26	11.52	5.74	78	78
13	Solution C	Immediately	7.53	4.62	2.91	73	34
14	+	After 2 days	10.69	6.92	3.77	72	48
15	alanin	After 7 days	16.56	10.45	6.11	95	75
16	(M/100)	Control, uncut	17.86	12.00	5.86	81	81
17	Solution C	Immediately	14.38	7.29	7.09	140	65
18	+ sodium	After 2 days	18.32	10.13	8.19	123	83
19	nucleinate	After 7 days	22.85	14.57	8.28	131	103
20	(⅒ per cent)	Control, uncut	25.43	15.09	10.34	115	115

* Per cent relative to corresponding culture, with respect to the time of excision of cotyledons, in the unmodified solution C.

paper (Duggar, '20) called solution C, which is one of the "best" combinations developed by Livingston and Tottingham ('18), and this solution has been shown to contain a favorable concentration of potassium nitrate for the growth of wheat and peas. Nevertheless, in spite of the fact that at the time of the excision of the cotyledons (even in those excised after only 2 days) there was considerable green leaf tissue in the seedlings, still the growth was weak, and at the end of 24 days the plants weighed less than one-half the control. The addition of glycocoll and of sodium nucleinate increased the growth quantities materially in the corresponding cultures, while the addition of sodium asparaginate or alanin was slightly depressing. The depressing action, however, may have been due to a small amount of bacterial decomposition products. Even in the presence of sodium nucleinate, as in culture 17, the amount of growth when the cotyledons were excised after 2 days is much less than in the control (cotyledons uncut) in solution C, culture 4. The data seem to indicate that no proper nutrient substitute for the cotyledons has been found in these organic substances. Some additional experiments in which sugar was used in connection with nitrogen-containing substances have not served to change materially the conclusions which may be drawn. In other experiments urea and nucleic acid were used, but neither of these has been as favorable as sodium nucleinate or glycocoll. It is true, however, that sodium nucleinate has increased more than any other compound thus far used the growth quantities in the cultures lacking cotyledons.

The importance of the cotyledons in the vigorous development of the seedling is an ancient observation. Bonnet (1754) demonstrated that beans and buckwheat grew less rapidly when the cotyledons were cut off, and more important still, he observed the persisting effect of this early difference, stating the matter in the following words: "La meme différence, ou une différence analogue, a subsisté entre ces Plantes pendant toute la durée de l'accroissement. Il a toujours été facile de distinguer les unes des autres."

Sachs ('59) observed the same fact a century later while devoting more attention to the physiology of absorption and nutrition. Discussing numerous experiments designed to determine the interdependence of organs and tissues in the embryo, Van Tieghem ('73) refers incidentally to the problem here discussed.

While Schmid ('94), Hannig ('04), and Smith ('07) have contributed many interesting observations regarding the nutrition of the embryo and the capacity of different parts to develop or regenerate, these facts do not closely relate to the present investigation. Dubard and Urbain ('13), however, emphasize the favorable effects of the endosperm of certain grains in the early stages of germination. They directed their work primarily toward determining the capacity of the embryos to develop in the absence of the endosperm.

Recently Andronescu ('19) has sought to determine the importance of the endosperm and scutella in *Zea Mays* and at the same time he has endeavored to find a substitute for these, also to follow in heredity any effects observed. While demonstrating that normal plants develop without endosperm, his use of the term normal is a relative one, and he concludes with the statement, "We cannot deny, however, that the presence of endosperms is beneficial in the process of germination, as well as in the further development of the plants."

The writer proposes to continue these investigations with plants grown under sterile conditions in the hope of determining more definitely the nature of the special nutrient or growth-inducing substance furnished by the cotyledons. At present one of several explanations for the failure to substitute readily for the cotyledons may be given: (1) it is conceivable that a combination of organic nutrients including several amino acids may be necessary for normal growth; (2) that penetration of organic substances may be slow and difficult; and (3) that the cotyledons may contain a vitamine requisite for the vigorous development of the plant. In any case the results so far obtained, as well as the observations of other investigators, indicate that the depression of growth accompanying the excision of the cotyledons is marked in the case of peas and other plants with fleshy seed-leaves, and that the influence of excision extends throughout the growth period of the plants.[1]

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[1] Since this paper was written there has appeared another article of considerable interest dealing with the effect of the endosperm upon the growth of the embryo (Urbain, A., Influence des matiéres de réserve de l'albumen de la graine sur le développement de l'embryon. Rev. Gén. Bot. **32**: 125–139, 165–191. *24 fig.* 1920.). In addition to careful observations on the effects of the excision of the endosperm on the development of a number of plants, a careful comparative study was made of internal structure.

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